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Citation for published version:

Froy, H, Börger, L, Regan, CE, Morris, A, Morris, S, Pilkington, JG, Crawley, MJ, Clutton-brock, TH, Pemberton, JM & Nussey, DH 2018, 'Declining home range area predicts reduced late-life survival in two wild ungulate populations', *Ecology Letters*, vol. 21, no. 7, pp. 1001-1009. <https://doi.org/10.1111/ele.12965>

Digital Object Identifier (DOI):

[10.1111/ele.12965](https://doi.org/10.1111/ele.12965)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Publisher's PDF, also known as Version of record

Published In:

Ecology Letters

Publisher Rights Statement:

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LETTER

Declining home range area predicts reduced late-life survival in two wild ungulate populations

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Abstract

Demographic senescence is increasingly recognised as an important force shaping the dynamics of wild vertebrate populations. However, our understanding of the processes that underpin these declines in survival and fertility in old age remains limited. Evidence for age-related changes in foraging behaviour and habitat use is emerging from wild vertebrate studies, but the extent to which these are driven by within-individual changes, and the consequences for fitness, remain unclear. Using longitudinal census observations collected over four decades from two long-term individual-based studies of unmanaged ungulates, we demonstrate consistent within-individual declines in home range area with age in adult females. In both systems, we found that within-individual decreases in home range area were associated with increased risk of mortality the following year. Our results provide the first evidence from the wild that age-related changes in space use are predictive of adult mortality.

Keywords

Ageing, fitness, home range, Isle of Rum, longitudinal study, red deer *Elaphus cervus*, senescence, Soay sheep *Ovis aries*, space use, St Kilda.

Ecology Letters (2018)

INTRODUCTION

Demographic senescence, the age-related decline in survival probability and fertility, is widely observed in nature and increasingly acknowledged as an important force shaping the ecological and evolutionary dynamics of wild vertebrate populations (Nussey *et al.* 2013; Bouwhuis & Vedder 2017; Lemaître & Gaillard 2017). Research in laboratory model systems demonstrates that these demographic patterns are underpinned by a complex and variable process of deterioration (Kirkwood 2005; Niccoli & Partridge 2012; López-Otín *et al.* 2013). However, our understanding of the processes responsible for senescent declines in natural populations remains limited (Nussey *et al.* 2013). Ecological traits such as foraging behaviour, habitat selection and space use represent potentially important proximate drivers of demographic variation because of their association with resource acquisition (Stephens *et al.* 2007; Gaillard *et al.* 2010). There is mounting evidence that space use and foraging behaviour may change in late life in wild birds and mammals (Catry *et al.* 2006; MacNulty *et al.* 2009; Montgomery *et al.* 2012). However, evidence directly linking such age-related changes in behavioural traits to reduced adult survival or fecundity are currently lacking in wild systems.

Space use is a complex, composite trait shaped by many non-mutually exclusive physiological, ecological and social factors that may vary with age (Nathan *et al.* 2008). As individuals get older, their increased experience and knowledge of the environment may result in reduced exploratory behaviour

and increased habitat selectivity, enabling them to forage more efficiently (Galbraith *et al.* 1999; Daunt *et al.* 2007). Social factors may also contribute to space use in many species, which could have a positive effect on resource acquisition if social dominance increases with age (Sherry & Holmes 1989). However, competitive exclusion may occur if individuals experience senescent declines as they move into late adulthood. Physiological declines associated with senescence could influence space use more directly, for example through declines in locomotor performance (Doherty 2003; Tanaka & Seals 2008; Labocha *et al.* 2015), or sensory and cognitive function (Barnes *et al.* 1980; Spear 1993). These processes could contribute to demographic senescence through negative impacts on resource acquisition. Several recent studies have documented late-life muscle and bone pathologies in wild mammals, which could impact locomotor function (Hindle *et al.* 2009a,b; Peterson *et al.* 2010; Arthur *et al.* 2015). Furthermore, a growing body of evidence reveals age-related changes in different aspects of space use, foraging behaviour and performance in wild birds and mammals (Saïd *et al.* 2009; Lecomte *et al.* 2010; Catry *et al.* 2011; Le Vaillant *et al.* 2013; Cunningham *et al.* 2017; Thurfjell *et al.* 2017). However, these studies have been unable to distinguish within-individual changes over the course of adulthood from important differences in space use and resource acquisition among individuals, which will also shape patterns of age-related variation (van de Pol & Verhulst 2006). Longitudinal data are required to tease apart these processes, and to link within-individual changes with fitness-related traits, thereby revealing the extent to

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which changes in space use may contribute to demographic senescence in natural systems.

Here, we used estimates of annual home ranges (Börger *et al.* 2008) in mature adult females to explore how space use varies with age using data from two long-term, longitudinal field studies: red deer (*Cervus elaphus* Linnaeus, 1758) on the Isle of Rum (Clutton-Brock *et al.* 1982), and the Soay sheep (*Ovis aries* Linnaeus, 1758) of St Kilda, Scotland (Clutton-Brock & Pemberton 2004). Both populations are unmanaged, and there are no natural predators on the islands. An individual's home range is therefore driven by a combination of habitat selection and intraspecific competition (Albon *et al.* 1992; Coulson *et al.* 1999). Previous studies of space use in these systems focused on lifetime estimates of home range or resource selection, and found considerable heterogeneity among individuals (McLoughlin *et al.* 2006; Stopher *et al.* 2012; Regan *et al.* 2015). One previous study looked at annual home ranges, and found that home range area declined with age in adult female Soay sheep, whereas a metric of habitat quality increased with age (Hayward *et al.* 2015).

In this study, we tested whether and how home range area and a measure of home range quality (the latter in Soay sheep only) changed with age within individuals, accounting for effects of selective disappearance. We then tested whether among- and within-individual variation in these metrics was associated with subsequent over-winter survival. We observed consistent patterns across both study systems: home range area declined with age, and within-individual reductions in home range area were associated with reduced subsequent survival probability. Harnessing the data on home range quality for Soay sheep, we compared observed results with three potential scenarios where different processes were responsible for within-individual changes in space use. First, if physiological declines or loss of dominance were driving the competitive exclusion of ageing individuals from high quality areas, we expected to observe within-individual declines in home range quality with age, which were associated with reduced survival probability. Second, if increases in foraging experience or social dominance were responsible for age-related changes in space use, we predicted that habitat quality would increase with age within individuals, which would be positively associated with survival probability. Finally, if senescent declines affecting locomotor function and resource acquisition were responsible for age-related changes in space use, we predicted within-individual declines in home range area with age that were associated with declines in over-winter survival probability, independent of habitat quality. This latter prediction is based on the expectation that physiological deterioration should limit activity levels and locomotor capacity of individuals generally, without necessarily impacting on habitat choice.

MATERIALS AND METHODS

The study systems

We used data from longitudinal field studies of two free-living ungulate populations on remote islands off the west coast of Scotland. Red deer living in the north management block of the Isle of Rum (c.1400 ha; 57°01' N, 06°17' W), and Soay

sheep resident in the Village Bay area of Hirta, on the St Kilda archipelago (c.230 ha; 57°49' N, 8°34' W), have been the subject of individual-based monitoring since 1971 and 1985 respectively (Clutton-Brock *et al.* 1982; Clutton-Brock & Pemberton 2004). Individuals in both populations are caught and individually marked shortly after birth, and subsequently monitored throughout their natural lives. We used data on adult females collected between 1974 and 2015 (Rum) and 1986–2015 (St Kilda).

Females conceive during the autumn rut, and offspring are gestated over winter. Female deer give birth to a single calf in late May–June, and Soay ewes to singleton or twin lambs in April. The vast majority of deaths are due to starvation in late winter (February–April). The survival and reproductive status of marked individuals is known from regular censusing (resighting probabilities > 0.93; Catchpole *et al.* (2000, 2004)). We defined 'deer year t ' and 'sheep year t ' running from 1 June year t to 31 May year $t + 1$ (Fig. S1). Demographic senescence is evident in both populations, with declines in adult survival, probability of reproduction, and offspring survival documented with increasing female age (Catchpole *et al.* 2004; Nussey *et al.* 2009; Hayward *et al.* 2015).

Regular censuses were carried out at both study sites, in which a fixed route was walked and the location of all individuals recorded to the nearest 100 m. An average of 40 censuses were conducted each year on Rum, and 30 each year on St Kilda, though censusing patterns were slightly more variable in the earlier study years (Fig. S2). On Rum, five monthly censuses were conducted in 8 months of each deer year: July, September, November (summer–autumn) and January–May (winter–spring). On St Kilda, ten censuses were conducted on each of three seasonal expeditions each sheep year: July–August (summer); October–November (autumn) and March–April (spring). Very few censuses were carried out in late May–June, meaning there was a natural break in censusing around the start of the new deer or sheep year on 1 June.

We chose to focus on adult females, since the determinants of space use are likely to vary markedly between the sexes in these polygynous systems, and their longer life spans may facilitate the detection of declines associated with senescence. Data availability is also greater for females, particularly on Rum where males tend to live outside the study area for much of the year. We included only individuals for which year of death was known in the analyses, so we could examine effects of longevity. Since we were interested in changes that occurred during adulthood, we restricted our analyses to females aged 5 and 3 years or more in deer and sheep respectively. This was when demographic rates plateaued as females moved into prime age (Catchpole *et al.* 2004; Nussey *et al.* 2009; Hayward *et al.* 2015), and corresponded to approximately 75% of female maximum lifespan in each population (excluding longest-lived c.2% of individuals in each case). On Rum, females that were culled when ranging outside the study area (< 10%) were excluded from all analyses to avoid bias, as individuals living towards the edge of the study area are disproportionately more likely to be culled and may have larger home ranges.

The vegetation in the Village Bay study area on St Kilda has been mapped on to a hectare grid. A number of major plant community types are present, the most productive being

the *Holcus–Agrostis* grasslands. *Calluna*- and *Nardus*-dominated wet-heath, and dryer *Calluna* heath, predominate in the less productive moorland areas (Jones *et al.* 2006). Between 2008 and 2012, complete species lists were compiled for the vascular plants within each hectare, and the percentage cover for each species assessed by eye (to the nearest 5%). There has been no detectable change in botanical composition within the communities since detailed botanical recording began in 1993 (Regan *et al.* 2015).

Data analysis

We used the census data to explore age-related variation in space use in female red deer and Soay sheep, aged 5 and 3 years and over respectively. We used kernel density methods to generate core annual home range estimates for individuals in both populations (Worton 1989; Fieberg & Börger 2012). We then examined how home range area (in hectares) changed with age in both species, and how an estimate of home range quality (% *Holcus lanatus* cover) varied with age in sheep. Finally, we looked at the relationships between home range area (and quality) and a key fitness component, annual survival probability.

Subsampling census data

There was variation in the number of census sightings of an individual in a given year. Because the number of census observations is associated with estimates of home range area (Fig. S3), we subsampled the census data to ensure that all individuals had an equal number of observations each year (Börger *et al.* 2006). Where an individual was observed more than once on a single census, only the first observation was retained. For deer, we considered only months where an individual was observed on three or more censuses, and randomly sampled 4 months without replacement. Where possible, months were sampled from both summer–autumn and winter–spring (94% of individual–years). Three observations were then sampled randomly without replacement for each sampled month, resulting in 12 locations for each individual in each year. For sheep, we considered only individuals that were observed at least three times in each seasonal expedition (summer, autumn and spring). Three observations were then sampled randomly without replacement for each expedition, resulting in nine locations for each individual–year. These sampling regimes were designed to maximise the repeatability of home range estimates for a given individual–year, while retaining sufficient sample sizes. We excluded the year of death for all individuals, so only years with complete census records were included. Each subsampling strategy was run 100 times, resulting in 100 subsampled data sets for both deer and sheep.

Estimating annual home ranges

We used kernel density methods to estimate annual home ranges for female deer and sheep using the package *adehabitatHR* (Calenge 2006) in R version 3.2.0 [R Core Team (2016)]. Subsampled census locations were jittered prior to the estimation of home ranges (the addition of a small amount of

noise) to avoid too many observations having identical grid references (since census locations were recorded to the nearest 100 m). The *href* method (termed the *ad hoc* method in *adehabitatHR*) was used to estimate the smoothing parameter for kernel estimation, since it provides conservative density estimates which are especially useful when the number of observations is low (Bowman & Azzalini 1997; Börger *et al.* 2006). The 70% isopleth was taken to reflect the core home range (Stopher *et al.* 2012; Regan *et al.* 2015). We estimated the annual core home range area in hectares for each individual in each of the 100 sampling runs, and calculated the repeatability for each individual–year to get an idea of sampling error. The repeatability of home range area among these 100 estimates was 0.840 (CI = 0.832–0.847) for deer and 0.804 (CI = 0.794–0.814) for sheep (calculated as the variance explained by the random effect of individual–year over the total variance from a mixed model of home range area). We then took the mean of these 100 estimates to be the annual home range area for a female in a given year. This resulted in 2555 estimates of annual home range area for 377 female deer, and 2226 estimates for 535 female sheep (mean 6.8 and 4.2 observations per individual respectively). The mean annual core home range area was 132.20 ± 156.54 SD hectares for female red deer, and 14.84 ± 14.67 SD for Soay sheep. Home range area was log-transformed prior to all analyses to ensure normality of residuals.

Home range quality in Soay sheep

We used the Village Bay vegetation map to generate estimates of annual home range quality for female sheep, based on the percentage cover of the grass species *Holcus lanatus* across the core home range. *H. lanatus* is a key component of the most productive grassland community on the island (Crawley *et al.* 2004), and the percentage cover of *H. lanatus* in a female's lifetime home range is positively correlated with her lifetime reproductive success in this population (Regan *et al.* 2015). The percentage cover of *H. lanatus* was calculated for each grid square contained within the core home range, and then the mean of these values was taken, weighted by the proportion of each grid square that fell within the home range. The percentage cover of *H. lanatus* was calculated for each of the 100 sampling runs, and the repeatability of this measure was calculated to be 0.916 (CI = 0.911–0.920) (variance explained by the random effect of individual–year over the total variance). The mean of the 100 estimates was taken to be the annual home range quality for a female in a given year (2226 estimates for 535 female sheep). Mean annual habitat quality was $34.93 \pm 12.77\%$ *H. lanatus* cover of the core home range.

Age-related variation in annual home range area and quality

Linear mixed effect models were used to characterise age-related variation in space use in adult female deer and sheep using the R package *lme4* v1.1-12 (Bates *et al.* 2015). Random intercept terms for individual and year were included in all models to account for repeated measures. We used a backwards model simplification approach, starting with a maximal model that included all fixed effects and sequentially removing

the least significant term from the model (linear effects were always retained if higher order terms such as quadratics were included). Significance was assessed using likelihood ratio tests. The maximal model included a fixed covariate for age (in years, linear and quadratic terms), and a fixed covariate for longevity (in years, linear and quadratic terms) to test for selective disappearance (van de Pol & Verhulst 2006). We also included a two-level factor for whether or not the home range measure was in the final full year of an individual's life to test for terminal shifts in space use as individuals approached death (Bouwhuis *et al.* 2009). A fixed factor was included for whether the female had a surviving calf or lamb on 1 October (0: no offspring; 1: offspring) to check that changes in space use were independent of changes in reproductive status. A fixed covariate for home range area was included in the model of sheep home range quality to test for changes with age that were independent of any age-related changes in home range area (correlation between home range area and home range quality $r = -0.72$, $P < 0.001$). Models with different fixed effects structures were compared using maximum likelihood estimation, but restricted maximum likelihood was used to estimate the final parameters presented. All continuous covariates were z-transformed prior to inclusion in models (mean = 0, SD = 1; Schielzeth (2010)). To check that our results were not influenced by changes in population density over the course of the studies, we re-ran all analyses including population size as a covariate in the models, but our results remained unchanged. We calculated the repeatability of home range area for individual females as the proportion of the total variance explained by the random effect for individual, and estimated the uncertainty around this estimate using parametric bootstrapping (1000 iterations) using the package *rptR* (Stoffel *et al.* 2017).

Associations between home range area and quality and survival

Bayesian generalised linear mixed effect models were used to test for associations between space use and annual survival probability using the package *MCMCglmm* v2.25 (Hadfield 2010). Female survival (year t : 1 June–31 May) was modelled as a binary trait using the threshold family and a probit link function (with the latent variables constrained to be between ± 7 to avoid numerical difficulties as the probabilities approached 0 and 1 respectively). Parameter estimates are presented as the posterior mode with 95% credible intervals of 2000 samples with minimal autocorrelation (1.1×10^6 iterations; 1×10^5 burn-in; thinning interval: 500). Random intercept terms for individual and year were included in all models to account for repeated measures.

Terms known to influence adult female survival in the two systems were included as fixed effects in our models. For deer, we included female age (linear and quadratic terms); a three-level factor for whether she gave birth to a calf in the current year t , and whether that calf survived to 1 October year t (did not give birth; gave birth but calf died; gave birth and calf survived); and a two-level factor for whether she had a surviving calf on 1 October year $t-1$ (0: no calf; 1: calf). For sheep survival, we included a fixed covariate for age (linear); and a two-level factor for whether she gave birth to a lamb in the

current year t (0: did not give birth; 1: gave birth). There were 3315 observations of 490 female deer, and 3158 observations of 725 female sheep (sample sizes were larger than for the analysis of age-related variation because we were able to include individuals that were still alive).

To test for associations between space use and survival, we included home range area for year $t-1$ as a fixed covariate in models of female survival year t for both deer and sheep. We then used a within-individual centring approach to decompose this effect into within- and between-individual contributions (van de Pol & Wright 2009). This involved including the average annual home range area across the data set for a given female (the between-individual effect), and the deviance of each observation from this average (the within-individual effect, calculated as observed minus average home range area). We also ran an alternative parameterisation of the same model, including the overall effect of home range area alongside the average home range area for a given female, which enabled us to test whether the within- and between-individual effects differed significantly (van de Pol & Wright 2009). For sheep survival, we also ran models including the overall effect of home range quality for year $t-1$, and then decomposed between- and within-individual effects of home range quality for year $t-1$. Finally, we tested the effects of both home range area and home range quality for year $t-1$ in the same model to see if they independently predicted female survival (both overall and decomposed effects).

RESULTS

Home range area declined with age in both systems (Table 1a and b; Fig. 1a and b). In Soay sheep, there was no association between home range area and longevity (quadratic effect LRT: $\chi^2_{d.f.=1} = 0.30$, $P = 0.585$; linear effect: $\chi^2_1 = 0.04$, $P = 0.833$), but in the deer there was evidence for a quadratic relationship, with females that died relatively younger or older having larger home ranges (Table 1a; Fig. S4). This selective disappearance was responsible for the increase in home range area observed at the oldest ages in the raw data means for deer (Fig. 1a; Fig. S5); there was no evidence for a quadratic association with age ($\chi^2_1 = 2.41$, $P = 0.121$). In both systems, there was no evidence for a terminal shift in home range area (deer: $\chi^2_1 = 1.45$, $P = 0.229$; sheep: $\chi^2_1 = 0.01$, $P = 0.910$). Our metric of sheep home range quality increased with age (Table 1c; Fig. 1c) up until the final year of life when it declined abruptly (Table 1c). The slope of the age-related increase in home range quality predicted by the model was shallower than seen in the raw data (Fig. 1c), since the model also accounted for the negative association between home range quality and home range area, which increased with age (Table 1c). There was also a positive association between home range quality and longevity (Table 1c; Fig. 1d). The repeatability of home range area for individual females over their lifetime was 0.747 (CI = 0.712–0.777) for deer and 0.509 (CI = 0.438–0.583) for sheep, and the individual repeatability of sheep home range quality was 0.842 (CI = 0.820–0.861) (Table 1).

In both study populations, within-individual declines in home range area were associated with reduced subsequent winter survival probability. Overall, there was a positive relationship

Table 1 Random and fixed effects estimates from the best linear mixed effect models for (a) deer home range area ($n = 2555$ observations of 377 females), (b) sheep home range area, and (c) sheep home range quality ($n = 2226$ of 535 females)

	Random effect	Variance	Fixed effect	Estimate	SE	P-value
(a) Deer HR area	ID	0.637	Offspring 1 Oct (1)	−0.190	0.020	< 0.001
	Year	0.017	Age	−0.073	0.012	< 0.001
	Residual	0.198	Longevity	−0.516	0.240	0.032
			Longevity ²	0.643	0.262	0.014
(b) Sheep HR area	ID	0.454	Offspring 1 Oct (1)	−0.084	0.035	0.016
	Year	0.216	Age	−0.006	0.055	0.910
	Residual	0.222	Age ²	−0.138	0.056	0.014
(c) Sheep HR quality	ID	78.789	Log (HR area)	−5.941	0.157	< 0.001
	Year	1.183	Age	0.542	0.140	< 0.001
	Residual	13.584	Final year (1)	−0.615	0.272	0.024
			Longevity	0.867	0.406	0.033

Covariates were z-transformed prior to inclusion in the models. Reference levels for factors are: Offspring 1 Oct (0); and Final year (0).

between adult female survival and home range area in red deer ($\beta = 0.136$, $CI = 0.058$ – 0.208 , $P < 0.001$), but there was no overall association in Soay sheep ($\beta = -0.043$, $CI = -0.114$ – 0.031 , $P = 0.268$). There was a positive relationship between survival and sheep home range quality ($\beta = 0.081$, $CI = 0.019$ – 0.149 , $P = 0.019$), which remained significant when the effect of home range area was accounted for ($\beta = 0.106$, $CI = 0.011$ – 0.198 , $P = 0.028$). Decomposing these relationships into differences between- and within-individuals indicated that there was a positive association between survival and mean home range area in female deer, and a stronger positive relationship with

within-individual deviance in home range area (Table 2a; Fig. 2a; difference between the within- and between-individual slopes $\beta = -0.145$, $CI = -0.300$ – 0.020 , $P = 0.074$). In sheep, the decomposition revealed opposing relationships for within- and between-components: there was negative relationship between survival and mean home range area, and a positive relationship with within-individual deviance (Table 2b; Fig. 2b; difference $\beta = -0.412$, $CI = -0.540$ – 0.0278 , $P < 0.001$). Similarly, there was a positive relationship between survival and mean home range quality, and a negative relationship with within-individual deviance (Table 2c; difference $\beta = 0.377$,

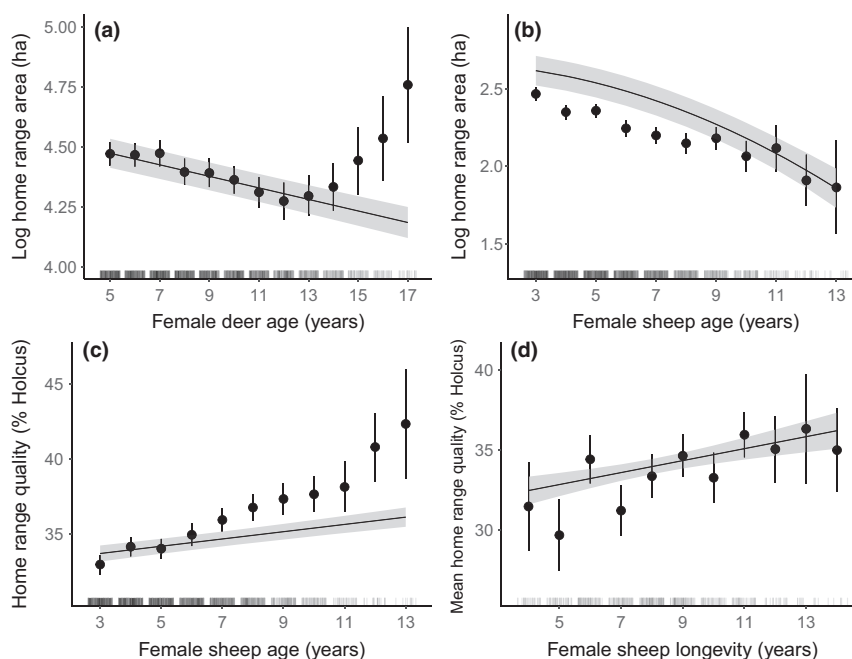


Figure 1 Relationships between female age and home range area in (a) red deer ($n = 2555$ observations of 377 females) and (b) Soay sheep ($n = 2226$ of 535 females); (c) female home range quality and female age and (d) female longevity and mean home range quality in Soay sheep. Points and bars show raw data means and associated standard errors. Black lines show predictions of best model with standard errors around this prediction in grey shading (see Table 1). Discrepancies between raw data means and model predictions are caused by other fixed effects which are accounted for in the models (see Results). For clarity, plots show only ages with 10+ observations, but analyses were conducted on the full age range. Rug plots on the inside of the x-axes show the distribution of the raw data.

Table 2 Random and fixed effects estimates from generalised linear mixed effects models for adult female survival in (a) red deer ($n = 3315$ observations of 490 females), and (b–d) Soay sheep ($n = 3158$ of 725 females)

			Posterior mean	Lower 95% CI	Upper 95% CI	pMCMC
(a) Deer HR area	Random	ID	0.108	0.000	0.402	
		Year	0.133	0.055	0.218	
	Fixed	Age	−0.205	−0.602	0.199	0.319
		Age ²	−0.410	−0.825	0.063	0.058
		Offspring 1 Oct t (calf died)	−0.409	−0.681	−0.168	< 0.001
		Offspring 1 Oct t (calf survived)	−0.706	−0.936	−0.523	< 0.001
		Offspring 1 Oct $t-1$ (1)	0.381	0.230	0.543	< 0.001
		Mean Log HR area $t-1$	0.084	0.005	0.166	0.045
(b) Sheep HR area	Random	ID	0.025	0.000	0.093	
		Year	0.530	0.218	0.893	
	Fixed	Age	−0.610	−0.699	−0.533	< 0.001
		Gave birth t (1)	−0.713	−0.939	−0.484	< 0.001
		Mean Log HR area $t-1$	−0.151	−0.219	−0.084	< 0.001
		Within Log HR area $t-1$	0.164	0.094	0.234	< 0.001
(c) Sheep HR quality	Random	ID	0.033	0.000	0.122	
		Year	0.519	0.231	0.861	
	Fixed	Age	−0.643	−0.737	−0.553	< 0.001
		Gave birth t (1)	−0.717	−0.968	−0.488	< 0.001
		Mean HR quality $t-1$	0.115	0.049	0.176	< 0.001
		Within HR quality $t-1$	−0.093	−0.158	−0.019	0.005
(d) Sheep HR area and quality	Random	ID	0.028	0.000	0.104	
		Year	0.526	0.214	0.905	
	Fixed	Age	−0.613	−0.708	−0.528	< 0.001
		Gave birth t (1)	−0.720	−0.956	−0.507	< 0.001
		Mean Log HR area $t-1$	−0.147	−0.257	−0.026	0.014
		Within Log HR area $t-1$	0.175	0.086	0.261	0.001
		Mean HR quality $t-1$	0.006	−0.101	0.111	0.904
		Within HR quality $t-1$	0.011	−0.068	0.104	0.812

The table shows the effects of between-individual differences in home range area or quality (mean log HR area or quality) versus within-individual change in home range area or quality (within log HR area or quality). Covariates were z-transformed prior to inclusion in the models. Reference levels for factors are: Offspring 1 Oct t (did not give birth); Offspring 1 Oct $t-1$ (0); and Gave birth t (0).

CI = 0.176–0.584, $P < 0.001$). However, when both home range area and home range quality were included in the model, only the within- and between-individual effects of home range area remained significant (Table 2d).

DISCUSSION

We have demonstrated that home range area declines with age in two ungulate systems, and that within-individual declines in home range area are associated with reduced subsequent survival probability (Fig. 1a and b; Fig. 2a and b). This represents, to our knowledge, the first evidence that age-related changes in space use are associated with adult survival in a wild animal. Home range quality data were only available for our Soay sheep system. Results combining home range area and quality data in the sheep are most consistent with a scenario in which age-related declines in home range area are driven by deterioration in locomotor, cognitive or sensory function and resource acquisition, because within-individual declines in home range area predicted survival prospects independently of changes in home range quality (Table 2d). The observed within-individual decreases in home range area and increases home range quality with age are unlikely to be

driven by competitive exclusion of senescent females by conspecifics. However, they are consistent with potential effects of increased experience and dominance over time, resulting in increased habitat selectivity. Whilst such improvements in foraging efficiency with age seem likely to be occurring in our study populations, our analyses do not support the prediction that this is associated with increases in adult survival. Although there was a positive overall association between home range quality and over-winter survival in female sheep, decomposing this relationship revealed that it was driven by among-individual differences: females with higher quality home ranges on average had higher survival probabilities (Table 2c). In contrast, within-individual increases in home range quality were actually associated with reduced survival probability. In both sheep and deer, within-individual declines in home range area were associated with reduced over-winter survival (Fig. 2). Although home range area and home range quality were correlated, when both effects were included in the survival model for sheep, only the effects of home range area were significant (Table 2d). Taken together, we feel this suggests that shrinking home range areas reflect some form of decline in physiological function, which in turn is associated with increased mortality risk.

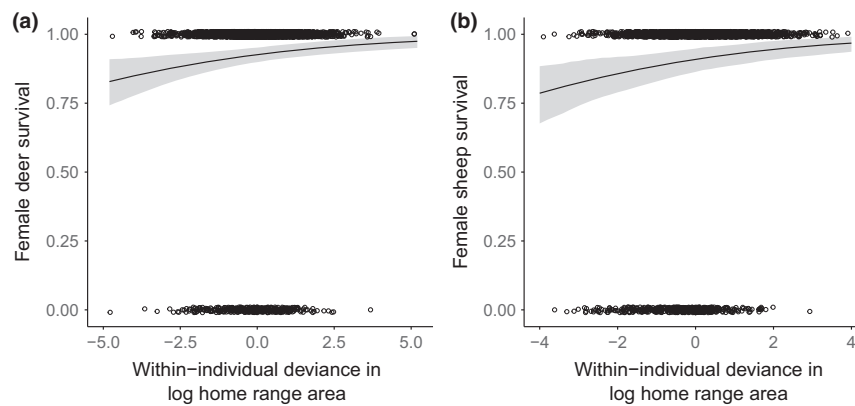


Figure 2 Relationships between within-individual deviance in home range area (calculated as observed minus mean home range area) and female survival in the subsequent year in (a) red deer ($n = 3315$ observations of 490 females) and (b) Soay sheep ($n = 3158$ of 725 females). Points show jittered raw data; black lines show model predictions and associated 95% confidence intervals in grey shading (see Table 2a and d).

Predation has been shown to profoundly influence ranging behaviour and habitat use (Creel *et al.* 2005; Valeix *et al.* 2009), but the absence of predation in these systems means that age-related variation in predation risk can be excluded as a cause of declining home range areas. Reduced mobility and activity levels in old age are well documented in humans and laboratory model organisms, as a result of declining muscle mass and strength (sarcopenia), joint flexibility, bone density and aerobic capacity (Doherty 2003; Short *et al.* 2005; Tanaka & Seals 2008; Riggs 1981), as are declines in spatial memory and visual acuity (Barnes *et al.* 1980; Spear 1993). The consistent pattern of decline in home range area we observed could therefore be the result of a similar deterioration in locomotor, cognitive or sensory function (Forster *et al.* 1996; Doherty 2003; Grotewiel *et al.* 2005). Alternatively, declining ability to obtain nutrients from ingested food, due to tooth wear or loss of digestive function (driven by increasing gastro-intestinal parasite burden) (Nussey *et al.* 2007; Hayward *et al.* 2009), could result in reductions in available energetic resources and locomotor activity. It is not possible for us to determine the exact physiological mechanism driving the age-related declines that we observe in this study. In future, the deployment of biologging devices capable of revealing much finer scale movement and behavioural patterns (Wilson *et al.* 2014), in combination with diet analysis and information on ingestion and metabolic rates (Turbill *et al.* 2011), could shed light on the mechanisms underpinning age-related changes in space use. However, the lines of evidence currently available to us suggest that within-individual declines in home range area are indicative of senescent declines, which may restrict resource acquisition in older individuals, with negative consequences for over-winter survival probability.

We used census data to characterise age-related variation in space use in two ungulate populations. These data were of relatively low temporal and spatial resolution in comparison to the kinds of data that are increasingly available with the advance of biologging technologies (Wilson *et al.* 2014). However, our census data were collected over many decades, enabling us to characterise space use across the entire lifespan for hundreds of individuals. This enabled us to separate within-individual ageing effects from the considerable

differences between individuals and, crucially, relate these within-individual changes to survival. To eliminate potential biases associated with variation in the number of census observations of an individual in a given year, we used a sub-sampling approach to equalise the number of observations. This resulted in 12 and nine observations per year for deer and sheep, respectively, which can still provide biologically relevant information on animal space use variation (Börger *et al.* 2006). Accordingly, our estimates of area and quality of the core annual home range were very consistent across random resampling of observations, and also highly repeatable across the adult lifetimes of individuals (proportion of variance explained by individual: 0.75 for deer home range area; 0.51 and 0.84 for sheep home range area and quality respectively). This strongly suggests that we were capturing a biologically relevant trait and a stable aspect of life-history. Furthermore, we detected clear and consistent declines in home range area with age in both red deer and Soay sheep. Our longitudinal data meant we could separate persistent among-individual differences, which may be generated by genetic or early-life effects, from changes associated with age. For example there was no overall association between home range area and survival probability in Soay sheep. Decomposing the relationship revealed a negative association with average home range area, which may be driven by the competitive exclusion of low quality individuals from areas with the best grazing, forcing them to range more widely, and a positive association with age-related changes in home range area (Table 2b). The longitudinal nature of our data enabled us to demonstrate that it was the within-individual declines in home range area that were associated with increased mortality risk in both systems, clearly illustrating the value of such data for furthering our understanding of potential drivers of demographic senescence in the wild.

Enhancing our understanding of the processes that underpin demographic senescence in natural populations is an essential step towards determining the causes of the considerable among- and within-species variation in ageing patterns recently observed in such systems (Nussey *et al.* 2013; Jones *et al.* 2014; Roach & Carey 2014). Our data provide the clearest evidence to date that the home ranges of individuals

shrink as they age, and this within-individual decline is predictive of reduced survival prospects in two wild populations. Further investigation is required to test how genes, environment and early life-history shape the onset and rate of shrinking home range area. Previous studies of both red deer and Soay sheep identify a highly asynchronous pattern of senescence across traits associated with reproduction, body condition and immunity, and argue for an integrative approach across phenotypes and physiological systems to understand senescence in wild systems (Nussey *et al.* 2009; Hayward *et al.* 2015). How declines in home range area correlate with changes in other important phenotypic traits, and to what degree these distinct phenotypic declines independently explain variation in demographic senescence, remain important questions.

ACKNOWLEDGEMENTS

Many thanks to Scottish Natural Heritage for permission to work on Isle of Rum National Nature Reserve, the National Trust for Scotland for permission to work on St Kilda, and QinetiQ and Kilda Cruises for logistical support. We are very grateful to all those involved in the long-term studies, particularly Ian Stevenson, Fiona Guinness and Martyn Baker, and to the Natural Environment Research Council, and the Biotechnology and Biological Sciences Research Council for funding.

AUTHORSHIP

HF and DHN conceived the study; HF conducted the analyses with support from LB and CER; AM, SM and JGP collected field data; MJC generated the vegetation map; TCB initiated the collection of quantitative data on ranging behaviour; TCB and subsequently JMP managed the long-term studies; HF and DHN wrote the manuscript, and all authors contributed to revisions and approved the final version.

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SUPPORTING INFORMATION

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Editor, Vanessa Ezenwa

Manuscript received 3 October 2017

First decision made 19 November 2017

Second decision made 25 February 2018

Manuscript accepted 15 March 2018